PHASCOLARCTID ORIGINS AND THE POTENTIAL OF THE SELENODONT MOLAR IN THE EVOLUTION OF DIPROTODONT MARSUPIALS

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ABSTRACT

Perameloids are regarded as ancestral to diprotodonts. Of known diprotodonts, the selenodont forms are structurally the best ancestors for the group. Dental and some cranial similarities between perameloids and selenodont diprotodonts are marked and indicate that bunodont diprotodonts such as burramyids are specialized derivatives of selenodont forms.

The majority of diprotodonts may be allocated into one of four groups based on dental morphology. Selenodont diprotodonts are probably monophyletic although two lineages can be recognized. Bunodont diprotodonts are almost certainly polyphyletic and contain forms with secondarily simplified molars. Ektopodont diprotodonts are monophyletic. Lophodont diprotodonts may be either polyphyletic or monophyletic.

Ektopodont diprotodonts have developed a type of lophodonty that is also partly developed in some phalangerids. This is achieved by a marshalling into rows of crenulations and conules. These transverse rows function as lophs and indicate one of perhaps three ways in which marsupial lophodonty could have been achieved.

It is commonly believed that bunodont burramyids such as *Cercartetus* are structurally the most primitive living diprotodonts (e.g. Tyndale-Biscoe 1973). *Phascolarctos* and other selenodont marsupials are regarded as specialized forms which probably evolved from ancestral bunodont diprotodonts. This view has been adopted in part because of the well-known secondary development of selenodonty in many eutherian groups (such as the origin of selenodont perissodactyls from bunodont condylarths) and in part because *Phascolarctos* and all other selenodont marsupials are assumed to be highly specialized leafeaters whereas bunodont diprotodonts are omnivores.

Recent basicranial (Archer 1976a) and dental investigations (Archer 1976b) of marsupicarnivores and perameloids have led to an alternative hypothesis presented here that selenodont diprotodonts evolved directly from perameloids and that they, not the bunodont diprotodonts, are structurally the most primitive.

The origin of marsupial lophodonty also requires new consideration in view of recently discovered Miocene diprotodonts. Ride (1971) has suggested an ingenious hypothesis for the origin of marsupial lophodonty which differs from the traditional view of Bensley (1903). The idea presented below is yet a third way in which the evolution of lophodonty in marsupials may have occurred.

Terminology of teeth is shown in Plate 52 and follows in part that used by Archer (1975a, 1975b). Basicranial terminology is that given by Archer (1976a). Family names follow the usage of Kirsch (1968).

PERAMELOIDS AND THEIR RELATIONSHIP TO DIPROTODONTS

Ride (1964) divides Australian marsupials into three orders: Marsupicarnivora, including dasyurids and thylacinids; Peramelina, including only the superfamily Perameloidea which contains peramelids and thylacomyids; Diprotodonta, including all ten families of Australian diprotodonts.

Molars of perameloids differ from those of marsupicarnivores mainly in having a very large stylar cusp C which is subequal in size to stylar cusp D, and in lacking a crest which directly links the paracone and metacone. Lacking this crest, the posterior protoerista links with stylar cusp C and the anterior metacrista links with stylar cusp D, thereby providing a transverse valley through which the hypoconid passes from the protoconal

basin to the buccal side of the tooth. The lower molars of perameloids differ from those of most marsupicarnivores in having a relatively high talonid and, in all groups (but particularly so in thylacomyids), a reduced paraconid.

The ways in which perameloid molars differ from those of marsupicarnivores are also the ways in which they are similar to molars of selenodont diprotodonts. Winge (1941) believes that the phascolarctid molar is structurally primitive among diprotodonts. The phascolarctid upper molar may easily be seen as a slightly modified perameloid molar. The modifications required to transform the upper molars of *Perameles* (a structurally ancestral peramelid) into upper molars of phascolarctids would be a reduction in size of the stylar cusps with approach of stylar cusp C to stylar cusp D, enlargement of the paracone and hypocone (the modified metaconule), greater development of the anterior and posterior cingula, and an increase in size of the metacone of M^4. All of the principal shearing crests are comparable in the two groups. To similarly transform the lower molars, the perameloid paraconid must be reduced, the crista obliqua must intersect and connect to the paracristid, and the paracristid must not contact the tip of the metaconid.

Perameloids, like diprotodonts but unlike marsupicarnivores, are syndactylous. For this reason perameloids (although polyprotodont) are regarded by most authors (e.g. Osgood 1921, Ride 1964) as the group most likely to have been ancestral to diprotodonts. Opponents of this view must hold that syndactyly has developed at least twice, once in perameloids and at least once in diprotodonts (Thomas 1888, Kirsch 1968). There is no evidence for this (Jones 1924) and the only recent examination of syndactyly (Marshall 1972) has failed to provide reasons for regarding syndactyly to have evolved more than once. It is to be expected that if perameloids are ancestral to diprotodonts, traces of this ancestry might be evident in the teeth and basicrania of structurally ancestral diprotodonts.

STRUCTURALLY ANCESTRAL DIPROTODONTS

Burramyids include living forms which are generally regarded (e.g. Thomas 1888, Troughton 1967, Tyndale-Biscoe 1973) as most closely resembling hypothetical ancestral diprotodonts. These authors refer to similarity in molar morphology to some marsupicarnivores such as dasyurids and also to their low chromosome number. This similarity consists of the subtriangular shape of the burramyid upper molar which lacks or has only a poorly-defined hypocone. Bensley (1903) regards these forms as indicative of an intermediate condition between ancestral tribosphenic marsupials which lack the hypocone and more advanced phalangerids which have well-developed hypocones. If burramyids are ancestral to phascolarctids, the latter must have redeveloped a complete stylar shelf as well as a majority of the shearing crests which, although absent in burramyids, are present in perameloids and marsupicarnivores. Alternatively, the burramyid condition could be a simplification of a more complex morphology such as that of phascolarctids and some petaurids, a view held by Winge (1941) and accepted here.

Of all 'possum' groups (phalangerids in the sense of Ride 1964; there is no corresponding taxon in the more recent classification of Kirsch 1968) the closely related phascolarctids and vombatids are also the only ones to have a variably developed alisphenoid-frontal contact on the side of the braincase, a feature found in all perameloids (Archer 1975b summarizes the distribution of this character in marsupials). Further, the 2N chromosome number of perameloids (not including thylacomyids) and vombatids is 14, and of phascolarctids 16, 14 being regarded as structurally primitive among marsupials (Sharman 1974). Serologically (Kirsch 1967, 1968), phascolarctids and vombatids are closely related, but perameloids group with dasyurids. However, the serological distance between phascolarctids and perameloids may be the result of relatively rapid protein evolution in phascolarctids (and vombatids).

At present, available evidence suggests phascolarctids (and possibly other selenodont forms) are the group best regarded as structurally ancestral to other diprotodonts.

DIVERSITY OF MOLAR PATTERNS AMONG DIPROTODONTS

With the exception of *Tarsipes* whose dental morphology is deceptively simple, presumably the result of degeneration from a more complex ancestral pattern, all diprotodont molars may be categorized as being either selenodont, bunodont, lophodont, or what may be referred to as ektopodont. With the exception of the ektopodont pattern (Plate 52), these types are figured by Bensley (1903).

SELENODONT DIPROTODONTS: Selenodont forms include all phascolarctids (*Phascolarctos, Perikoala, Pseudokoala, Litokoala*) some petaurids (*Pseudocheirus, Hemibelideus*, and *Schoinobates*) and possibly vombatids (*Vombatus, Lasiorhinus, Phascolonus, Rhizophascolonus*) to judge from

unworn teeth. It has been suggested (e.g. by Kirsch 1968) that phascolarctids and selenodont petaurids represent separate lineages, the development of selenodonty in the two lineages possibly being the result of convergence. Bensley (1903), and Turnbull and Lundelius (1970) point out significant differences in molar form in the two groups. However, it is also possible that the two groups had a common selenodont ancestor, differences noted in the modern representatives being nothing more than specialization developed later by each group. Bensley (1903) regards the *Phascolarctos* molar pattern as a derivative of the *Pseudocheirus* condition, while Winge (1941) interprets a structural trend which goes from *Phascolarctos* to *Pseudocheirus*. Kirsch (1967, 1968) has shown that serologically *Phascolarctos* groups with vombatids rather than the other selenodont forms which group with the remaining diprotodonts. If phascolarctids (and vombatids) have undergone rapid protein evolution relative to other diprotodonts, their serological uniqueness could obscure relationships that may exist with other selenodont diprotodonts. Sharman (1974) notes that because *Phascolarctos* has $2N = 16$ chromosomes, it is closer to the assumed primitive number of 14, and differs from other selenodont diprotodonts which range from 20 to 22. The significance of this is difficult to interpret in view of the fact that within one family (the macropodids), the range is 10 to 32.

In view of the generally held notion (Troughton 1967, Ride 1970) that selenodont diprotodonts are strictly herbivorous, it seems appropriate to point out here that Common Ringtails (*Pseudocheirus peregrinus*) held in captivity by the author invariably show a decided preference for insects if given a choice between these and any type of leaf or fruit.

BUNODONT DIPROTODONTS: Bunodont forms include some petaurids (*Petaurus, Gymnobelideus,* and *Dactylopsila*), burramyids (*Acrobates, Distoechurus, Cercartetus,* and *Burramys*), phalangerids (*Trichosurus, Wyulda,* and *Phalanger*), potoroine macropodids (*Hypsiprimnodon, Bettongia, Caloprymnus, Aepyprymnus, Potorous,* and *Propleopus*), and thylacoleonids (*Thylacoleo* and *Wakeleo*). Bensley (1903) regards the more tritubercular forms such as *Distoechurus* to be structurally ancestral to other bunodont diprotodonts, considering the absence of a hypocone to be structurally primitive. He also suggests that bunodont and selenodont forms may have been independently derived from tritubercular (Bensley's hypothetical properamelid) ancestors. This seems doubtful considering that selenodont and bunodont diproto-

todonts have many characters in common such as diprotodonty, reduced upper incisor number, wrinkled enamel, fasciculus aberrans, serological characters, and highly modified basicranium involving fusion of the ectotympanic (although fusion does not occur in some *Phascolarctos*) which are not present in known tritubercular groups. It seems more reasonable to regard selenodont and bunodont diprotodonts as having been derived either from one another or from other diprotodont ancestors, rather than independently derived from tritubercular ancestors. Winge's (1941) view, that bunodont forms were derived from selenodont forms, is accepted here because of the presence of traces of selenodonty and the common occurrence of wrinkled enamel in bunodont diprotodonts. This interpretation implies that the more tritubercular and less selenodont forms such as *Distoechurus* are in fact highly specialized forms, and not, as Bensley (1903) believes, structurally primitive.

The unity of the bunodont diprotodonts is very doubtful and several independent origins, possibly from selenodont forms of different sorts, are probable. Bunodont non-macropodids have a 2N chromosome number of 14 to 20 (Sharman 1974). *Phalanger*, regarded here as a structurally primitive bunodont form, has 14 but so do burramyines which are regarded here as structurally advanced. Kirsch (1967, 1968) also regards the bunodont forms to represent several distinct serological groups.

EKTOPODONT DIPROTODONTS: Ektopodont forms are represented by the late Miocene species *Ektopodon serratus* (Stirton, Tedford and Woodburne 1967). They are characterized in part by transverse serrate ridges formed by numerous small upside down V-shaped longitudinal crests. *Ektopodon* was originally described as a possible monotreme, but Woodburne (pers. comm.) suggests it is a diprotodont following the discovery of an older and simpler species.

LOPHODONT DIPROTODONTS: Lophodont forms include macropodine macropodids and diprotodontids. Traditional views of the origin of lophodonty from bunodonty (such as proposed by Bensley 1903) involve evolution of crests or lophs which link the protocone to the paracone and the hypocone to the metacone. In lower molars it is generally assumed that the paracristid and paraconid become reduced, the metacristid develops as the anterior lophid, and the hypocristid develops as the posterior lophid. The crista obliqua becomes the midlink of macropodines.

The importance of *Ektopodon* in the present context is that it demonstrates that diprotodont lophs may not be homologues of the crests of other marsupials. Thomas (1888, p. 193) notes that in some species of *Phalanger* the molars have distinct transverse ridges. These transverse ridges could be regarded as incipient lophs. Close inspection of unworn molars reveals a striking similarity to molars of *Ektopodon*. The buccal half of the transverse ridges of upper molars and the lingual half of the ridges of lower molars appear to consist of numerous upside-down V-shaped longitudinal crests. The lingual half of the transverse ridges of upper, and the buccal end of the transverse ridges of lower molars consist of short steep-sided ridges which appear to be the homologues of ridges in these positions of molars of *Phascolarctos*. The remainder of the crown surface of *Phalanger* molars are covered in small wrinkles and crenulations, as are the teeth of selenodont and many bunodont diprotodonts. This suggests the possibility that lophs may have evolved through a marshalling together of wrinkles, conules and small ridges already present in ancestral selenodont forms. Overriding this organization in *Phalanger*, as in most bunodont forms, are the remnants of selenodont crests, now modified to form triangular buttresses at the ends of transverse lophs. This transformation is as readily performed on lower as it is on upper molars.

In completely lophodont forms, the lophs are not clearly modified ancestral ridges. It is possible that marsupial lophodonty evolved more than once and in very different ways. Ride's (1971) interesting hypothesis for origin of macropodine molars assumes that a tritubercular pattern was ancestral to the lophodont pattern, that stylar cusps became the buccal ends of the upper lophs, and the paracone and metacone were incorporated along the length of the lophs. An alternative is that the lophodont molar has been derived from a selenodont molar in the manner outlined above. Lateral selenes became triangular buttresses (homologues of which occur in many macropodids), and transverse lophs were formed by a marshalling of conules, ridges and wrinkles. The already well-developed hypocones, reduced paraconids, and enlarged M4 of selenodont forms could have been characters directly utilized by ancestral lophodont forms. If this latter hypothesis for the origin of lophodonty is accepted, bunodont potoroine macropodids could be regarded as derivatives of lophodont macropodines, a conclusion also accepted by Ride (1971).
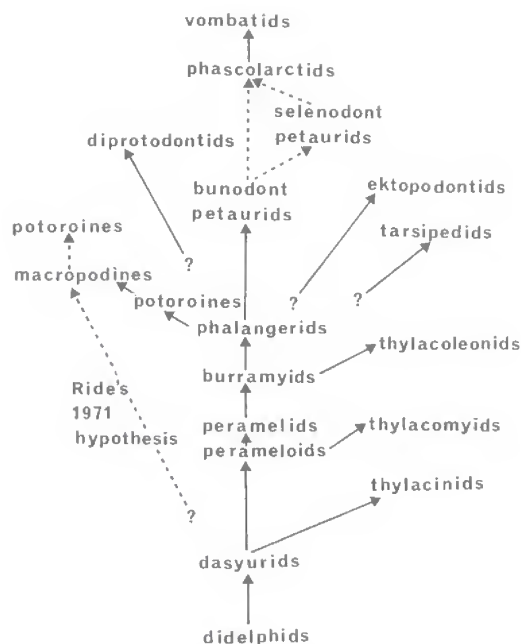

FIG. 1: Some traditional concepts of origins for Australian marsupial families. The two macropodid subfamilies are treated separately. These concepts are based largely on Bensley (1903) with modifications suggested by later authors. Wynyardiids are not shown because their teeth are unknown. Dashed lines indicate alternative origins, such as Ride's (1971) hypothesis for the origin of macropodids.
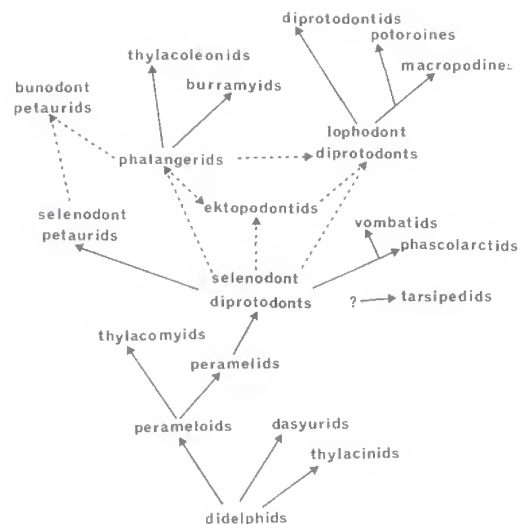

FIG. 2: Concepts of origin suggested in the present work. Alternatives are indicated by dashed lines.

CONCLUSIONS

Various views of descent noted above are contrasted in Figs. 1–2. It is suggested here (as shown in Fig. 2) that selenodont diprotodonts arose directly from peramelids and were the base stock for all other diprotodont radiations.

The relationship between ektopodontids and other diprotodonts is unclear. They exhibit a transverse lophodont molar pattern which, although possibly convergent on other lophodont forms and derived from phalangerids, indicates a unique way in which lophodonty could be developed from selenodonty.

It is not clear how lophodonty was achieved in macropodids or diprotodontids. It could have developed from either the bunodont, ektopodont, or selenodont pattern. Ride (1971) suggests the additional possibility that lophodonty developed as a modification of a more or less tribosphenic pattern.

ACKNOWLEDGMENTS

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